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Warren C. Conway

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Research Paper

## Identifying the migratory strategy of the Lower Colorado River Valley population of Greater Sandhill Cranes

Courtenay M. Conring<sup>1,2</sup>, Kathryn Brautigam<sup>1</sup>, Blake A. Grisham<sup>1</sup>, Daniel P. Collins<sup>3</sup> and Warren C. Conway<sup>1</sup>

<sup>1</sup>Department of Natural Resources Management, Texas Tech University, <sup>2</sup>Alabama Department of Conservation and Natural Resources, <sup>3</sup>U.S. Fish and Wildlife Service, Southwest Region

**ABSTRACT.** Across North America, Sandhill Cranes (*Antigone canadensis*) use an array of migratory strategies, ranging from “jumping,” or taking 1 or 2 flights from wintering grounds to a staging area, then on to the breeding grounds, to “hopping,” or taking shorter flights among multiple (>3) staging areas between termini. We captured 16 adult and 2 juvenile Greater Sandhill Cranes (*Antigone canadensis tabida*) from the Lower Colorado River Valley population (LCRVP) and fitted them with platform transmitter terminals (PTTs) for GPS satellite telemetry. We used recorded locations and Brownian bridge movement models (BBMMs) to identify migration corridors and areas of migratory use (AMUs) during spring and fall migration (2014-2016). Eighty-nine percent of our sample (n = 16) of LCRVP Sandhill Cranes with PTTs flew direct paths between summer and winter termini. Starting in the Great Basin and moving into the Mojave Desert and then into the Sonoran Desert, the LCRVP aligned its migration with drainages, rivers, and reservoirs. Within those direct paths, we identified 18 unique and discrete AMUs along an ~1000-km corridor and 3 within minor corridors taken by the other 2 cranes. We defined AMU as an area within a crane’s 75% BBMM migration confidence contour where the crane had 2 or more subsequent time stamps (could be ≥3 hours) and did not travel >40 km from the first time stamp. The average migration duration was 23 days (spring, n = 3; fall, n = 2; cranes, n = 53). The fact that many individuals stopped several times after relatively short flights during both migration seasons suggests that the LCRVP generally uses a “hop” migration strategy. The use, often frequent and consecutive, of the 21 AMUs in this research reveals the potential importance of these migration areas to the LCRVP for its social, behavioral, and energetic requirements during migration.

## Détermination de la stratégie de migration adoptée par les Grandes Grues du Canada appartenant à la population de la vallée du Colorado inférieur

**RÉSUMÉ.** En Amérique du Nord, la Grue du Canada (*Antigone canadensis*) a recourt à diverses stratégies de migration, allant des « grands sauts », c'est-à-dire d'effectuer un ou deux vols de l'aire d'hivernage à une halte printanière pour ensuite se rendre à l'aire de nidification, aux « petits bonds », soit d'entreprendre des vols plus courts entre plusieurs haltes (>3) jusqu'à la destination finale. Nous avons capturé 16 adultes et 2 jeunes Grandes Grues du Canada (*Antigone canadensis tabida*) appartenant à la population de la vallée du Colorado inférieur (PVCi) et les avons munis d'une balise radio avec télémétrie satellitaire GPS. Nous avons utilisé les positions enregistrées et des modèles de déplacement fondés sur le pont brownien (MDPB) pour déterminer les corridors de migration et les secteurs utilisés en migration (SUM) printanière et automnale (2014-2016). Quarante-neuf pourcent de notre échantillon (n = 16) de grues équipées de balise ont parcouru des trajets directs de leur aire de nidification à leur aire d'hivernage. Au départ du Grand Bassin, les grues de la PVCi ont transité par le désert de Mojave, puis le désert du Sonora, suivant les bassins hydrographiques, les rivières et les réservoirs. Parmi ces trajets directs, nous avons repéré 18 SUM uniques et distincts le long d'un corridor d'~1000 km et 3 dans des corridors secondaires aussi utilisés par les deux autres grues. Nous avons défini un SUM comme étant l'aire contenue à l'intérieur du couloir migratoire d'une grue délimitée par la ligne de contour obtenue avec le MDPB à un niveau de confiance de 75 % et où au moins deux positions subséquentes ou plus (pouvant être de ≥3 heures) ont été enregistrées, montrant un déplacement de >40 km depuis la première position. La durée moyenne de migration était de 23 jours (printemps, n = 3; automne, n = 2; grues, n = 53). Le fait que de nombreux individus soient arrêtés plusieurs fois à la suite de vols relativement courts durant les deux migrations saisonnières semble indiquer que les grues appartenant à la PVCi utilisent habituellement la stratégie de migration par « petits bonds ». L'utilisation souvent fréquente et consécutive des 21 SUM identifiés dans le cadre de cette étude révèle l'importance possible de ces secteurs pour combler les besoins sociaux, comportementaux et énergétiques de la PVCi au cours des migrations.

**Key Words:** Lower Colorado River Valley; migration; migration strategy; migratory corridor; Sandhill Cranes

## INTRODUCTION

Migration is a behavioral adaptation for exploiting temporal peaks of resource abundance and avoiding temporal resource depression (Alerstam et al. 2003, Winkler et al. 2014). Resource availability is

geographic and temporally variable during migration, and as such, migratory birds typically adjust their migration strategy with the associated changes in resource abundance. Although multiple migration strategies exist, for discussion purposes, a simplified

categorization is provided by Piersma (1987) who defined three migration strategies: hop, skip, and jump. Although the traditional definitions have been altered and expanded given new data, the original definitions are as follows: hop is defined as traveling short distances between sequential sites and accumulating small amounts of extra fuel (food) when stopped; skip is defined as traveling longer distances between sequential sites and accumulating medium amounts of extra fuel; and jump is defined as traveling long distances (thousands of kilometers) between sequential sites and accumulating large amounts of extra fuel (Piersma 1987, Warnock 2010). Warnock (2010) suggested that duration of stay at stopover or staging sites, predictability of food resources, and foreseen obstacles are all correlated with these strategies. These strategies can be depicted as concepts along a continuum with a single migratory flight between breeding and wintering termini at one extreme, and multiple short flights between multiple suitable stopover locations at the other extreme of the strategy spectrum. Hopping and skipping result in short (hours or days) stays between short flights, whereas jumping usually results in longer (weeks or months) stays between longer flights at staging areas where food sources are reliable and abundant (Warnock 2010). These migration strategies are associated with different stopover behaviors and typically are correlated with total migration distance and amount of extra fuel intake at stopovers. Abiotic factors, such as stochastic weather events or environmental conditions, e.g., storm and flood, can potentially affect time spent at a stopover.

Sandhill Cranes (*Antigone canadensis*; also cranes) migrate in multiage groups, typically composed of multiple family groups (2 adults and 1 or 2 juveniles; Holmgren et al. 1993, Restani 2000, Galván 2005) and subadult groups (2-3 years old). The family groups stay together during the colt's first fall migration and winter, minimizing risks associated with inexperienced migration of juveniles (hatch year; Tacha 1988). Sandhill Cranes, like other migratory game birds, are categorized into management units, or populations, based on their distribution, which includes their winter, summer, and migration ranges. Many aspects of migration, e.g., distance, duration, phenology, and so forth, vary widely among crane subspecies and migratory populations. For example, cranes from the midcontinent population (MCP), composed of both *Antigone canadensis tabida* (Greater Sandhill Crane, also greater) and *Antigone canadensis canadensis* (Lesser Sandhill Crane, also lessers), are long-distance migrants that exhibit a jump strategy (Warnock 2010) with major staging areas along the Platte River in Nebraska and in Saskatchewan (Lovvorn and Kirkpatrick 1981, Krapu et al. 1984, Fronczak 2014, Krapu et al. 2014). The MCP breeds as far north as eastern Siberia and winters as far south as Mexico, with known migrations ranging from ~2000 to more than 7000 km between termini, taking at least 2 months to complete in most cases (Krapu et al. 2014). Another relatively long-distance migratory population consisting of both lessers and greater is the Pacific coast population. However, cranes from the Pacific coast population take only about 27 days to migrate 3600 km between breeding and wintering grounds (Petrula and Rothe 2005), use either a hop or skip migratory strategy, and make many stops during both spring and fall migrations (Ivey et al. 2005). These 2 populations alone demonstrate the migratory heterogeneity found in the species, and research is slowly revealing where the remaining populations' strategies fit along the spectrum.

Research aimed at gaining a basic understanding of the migratory ecology of the 3 intermountain populations (Central Valley, Lower Colorado River Valley, and Rocky Mountain) is ongoing. Specifically, the Lower Colorado River Valley population (LCRVP), one of the least studied of all the migratory populations, has experienced increased interest in determining the migratory strategy of the population in recent years (Collins et al. 2016). Compared with the midcontinent and Pacific populations, the LCRVP is far less abundant with a 3-year average of 2509 cranes (Dubvosky 2018); cranes from the LCRVP have shorter distances between seasonal termini to traverse and are known to take less time to complete migration (Collins et al. 2016). Given the long-distance flights of midcontinental cranes (~700-1000 km; Krapu et al. 2014; K. J. Brautigam, Texas Tech University, *unpublished data*) completed in ~1 day, effectively nullifying the need for fuel during migration, we expect a crane from the LCRVP to have the phenotypic requirements, both genetic and environmental, to complete migration between seasonal termini of relatively short distances (500-1000 km) with little to no stopping. However, although not explicitly stated in the literature, based on stopover and staging research (D. Collins, *personal observation*), it appears that cranes from the LCRVP generally exhibit the "hop" migration strategy (Piersma 1987, Warnock 2010).

Bird populations that use the hop migration strategy tend to travel comparatively short total migration distances over land; tend to have relatively continuous, predictable, and reliable food resources available along their migratory corridor; and tend to not travel over large geographic barriers (Warnock 2010). The LCRVP summer range includes northeastern Nevada and parts of Idaho and Utah; the winter range includes southwestern Arizona and southeastern California; and the ecosystem between termini is primarily the Great Basin, but also portions of the Mojave Desert and the Sonoran Desert. The LCRVP occupies the spatial gap between the other two western crane populations, the Rocky Mountain and Central Valley populations (Fig. 1). The three populations intermix (Collins et al. 2016) but are currently managed and identified as separate entities. Causal mechanisms that facilitate population mixing, i.e., overlap in breeding distribution, intermingling during migration, and so forth, have been observed, and the spatial arrangement of termini and food resources anecdotally suggest intermixing may occur via hopping within their combined distributions. Understanding the extent of the migration corridors, stops, and movement patterns for the LCRVP is imperative for habitat management but also provides a unique opportunity to assess if migration is one causal mechanism responsible for population intermixing in the Intermountain West. Our objectives were to identify the migration strategies for cranes from the LCRVP and locate areas of migratory use (AMUs) along the migration corridor.

## METHODS

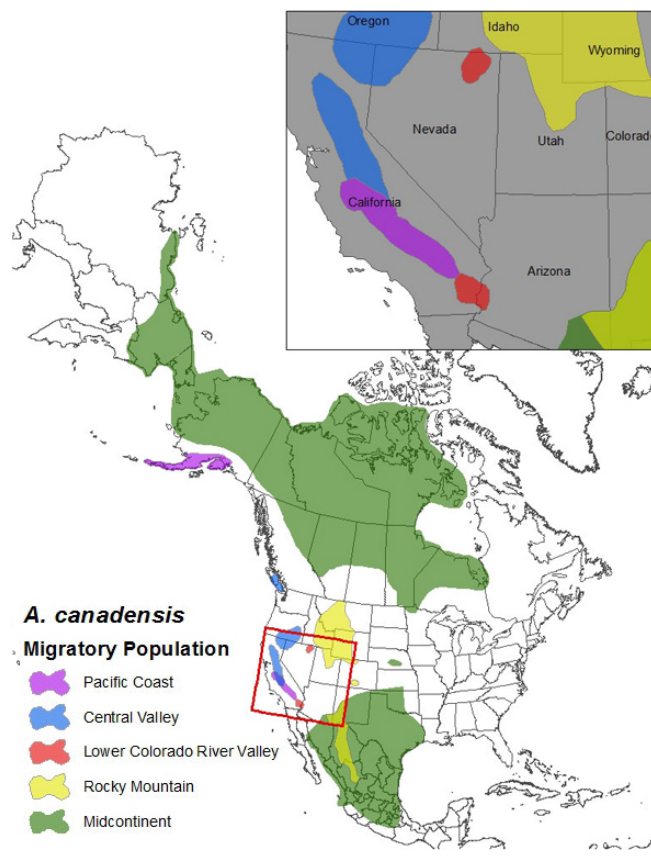
### Study areas

#### Geographic range

Nearly the entire geographic range and migration corridor of the LCRVP lies within the Great Basin, the largest contiguous watershed in North America. This vast watershed is ~542,000 km<sup>2</sup> and extends across most of Nevada, the western half of Utah, and portions of California, Oregon, Idaho, and Wyoming. The

ecosystems found there include sagebrush, warm and cold deserts, salt flats, riparian and playa wetlands, montane shrublands and timberlands, pinyon-juniper communities, and many other elevation- and slope-specific ecosystems found at elevations between -86 m (Death Valley) and 4421 m (Mt. Whitney). Sites were chosen by collaborators and agency biologists because of access to fields on and near federal refuges and crane presence during weeks leading up to capture in January 2014.

**Fig. 1.** Sandhill Crane (*Antigone canadensis*) population map, with the Lower Colorado River Valley population distribution in upper right inset.



### Cibola and the Lower Colorado River Valley

The Cibola National Wildlife Refuge (NWR) is 6729 ha and is located 69 m above sea level in the Colorado River floodplain, better known as the Lower Colorado River Valley (LCRV), and it is surrounded by Sonoran Desert ridges (Carver and Caudill 2007). Cibola NWR runs alongside 19.3 km of the Colorado River and contains 16 km of backwater from the Colorado River (U.S. Fish and Wildlife Service [USFWS] 2013b, 2017). The main land cover types of the refuge include agriculture, i.e., alfalfa (*Medicago sativa*), winter wheat (*Triticum aestivum*), and corn (*Zea mays*); the Lower Colorado River; moist-soil management units; salt cedar (*Tamarix* spp.) stands; cottonwood-willow stands (*Populus fremontii*, *Salix exigua*, and *S. gooddingii*); and desert shrub scrub (USFWS 2013a). Mean low and high temperatures for spring, summer, fall, and winter are 13-31°C, 23-41°C, 14-31°C, and 5-20°C, respectively (U.S. Climate Data 2014). Yearly

rainfall rarely exceeds 5.1 cm, with the peak rainfall occurring December through February (USFWS 2013a, U.S. Climate Data 2014). Sandhill Cranes use Cibola NWR during winter along with the rest of the LCRV that has similar habitat, including alfalfa, corn, and winter wheat fields belonging to private owners or the Colorado River Indian Tribes.

### Sonny Bono Salton Sea and Imperial Valley

The Sonny Bono Salton Sea NWR is 15,240 ha located in the Imperial Valley just south of the Salton Sea and 64 km north of the Mexico border (USFWS 2013b). Nearby cities include Calipatria to the east and Westmorland to the south. Despite being in the Sonoran Desert, the refuge receives water via agricultural runoff and irrigation from the Colorado River and serves as a consistent wintering ground for Sandhill Cranes (USFWS 2013b). Common habitat types found on the refuge include agricultural fields (alfalfa, wheat, rye grass [*Lolium perenne*], milo [*Sorghum bicolor*], millet [*Pennisetum glaucum*], and sudan grass [*Sorghum × drummondii*]), moist-soil management units, permanently flooded wetlands, and tree rows (USFWS 2013b).

The Imperial Valley is located in Imperial County in southeast California and stretches 80 km from the southern tip of the Salton Sea to the Mexican border (Eneva et al. 2012). Much of the area in the Imperial Valley is managed for agriculture. More than 100 different commodities are produced by farmers throughout the valley, many of which are valuable forage for cranes (Reinecke and Krapu 1986, Iverson et al. 1987, McIvor and Conover 1994, Imperial County Farm Bureau 2017). Abundant waste grain is available in the Imperial Valley fields and granaries (Iverson et al. 1985, 1987, Sudgen et al. 1988). The mean temperature in the Imperial Valley is 13°C in the winter and 32°C in the summer. Yearly rainfall in the Imperial Valley is ~9 cm, and the majority of the rain occurs in the winter and early spring (Johnson et al. 2009).

### Long Valley, Idaho

Located in west-central Idaho approximately 100 km north of Boise, Idaho, Long Valley (44.52°N, 116.05°W) follows alongside the Payette River. The river weaves through the broad, flat, glaciated valley dominated by agricultural grasslands and dense riparian stands of lodgepole pine (*Pinus contorta*), surrounded by mountain ranges on all sides consisting of ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis*), and Douglas fir (*Pseudotsuga menziesii*; Van Daele and Van Daele 1982). Lake Cascade, Payette Lake, and Little Payette Lake are located in the area.

### Field methods

#### Capture

We chose trapping locations based on previous crane use during the days leading up to capture efforts in early January 2014. We set up rocket nets in partially mowed corn fields after we identified trapping locations in Cibola NWR and a granary just south of Brawley, California, in the Imperial Valley. Typically, we fired rockets when ~12 cranes were within the capture target. We placed cranes in burlap sacks for processing to prevent capture myopathy. We banded each crane with a size-9 USGS-issued aluminum band on its right tibiotarsus and fit select adults with a global



positioning system (GPS) satellite platform transmitter terminal, or PTT (Microwave Telemetry Inc. [MTI], Columbia, Maryland, USA; white alphanumeric code, X00-X19, on black background), on their left tibiotarsus with the antennae pointed toward their feet and solar panels forward. We identified adults using head plumage characteristics (Lewis 1979). We collected the following information for each capture: location, method, bird identification (ID) number, band ID, age (after hatch year/hatch year), and transmitter ID for selected adults. We only tagged the largest adult in each family unit in an effort to (1) achieve the relatively smallest excess-weight burden and (2) remotely follow only 1 crane in each group and avoid pseudoreplication. We did not attempt to identify sex of captured or tagged cranes, which requires collecting blood, because our objectives did not warrant it.

### Location data

We programmed PTTs to collect 4 GPS locations each day (0000, 0700, 1000, and 1500 hours) and record latitude, longitude, speed, course, and altitude at each location. We downloaded GPS data weekly from the ARGOS website (<https://argos-system.clsamerica.com/cwi/Logon.do>) and parsed it into KML and text files using MTI GPS data parsing software. Locations that were lost or compromised because of drained batteries or used two-dimensional fixes, no fix, or low voltage to collect data were removed from analyses. In-flight locations were removed from the AMU analyses to ensure cranes were on the ground at the time of the location fix. Altitude was recorded by the PTTs for every location, but the PTT we used rounded the altitude up or down to the nearest 10 m (e.g., 10, 20, 30), which is the difference of being on the ground or in-flight in some scenarios. Speed, which is only recorded when the crane is in motion, was the parameter used to distinguish locations when a bird was in flight instead. Speeds >10 knots were considered to be in-flight and removed.

## Statistical and ArcGIS methods

### Migratory corridors

We used a Brownian bridge movement model (BBMM) to develop migratory pathways represented as probability of use/presence contours. We truncated our data sets to include only points between breeding and winter seasons (Horne et al. 2007, Sawyer et al. 2009, Nielson et al. 2013) to delineate migration corridors. One similar movement analysis is the dynamic Brownian bridge movement model (dBBMM), which for some objectives is more accurate for migratory species (Kranstauber et al. 2012). However, we ultimately used results from the “BBMM” package in the program R (Horne et al. 2007, Sawyer et al. 2009, Nielson et al. 2013; R version i386 3.0.2, <http://www.r-project.org>) because dBBMM was not able to magnify migration corridors as a result of overwhelming nonmigration data, but BBMM used a simpler algorithm and was able to draw migration corridors by estimating the path taken between locations. We used all migratory locations (Appendix 1) from the initial trapping through the point of transmitter failure or the conclusion of the spring 2016 migration. We used known breeding grounds and wintering grounds for individual cranes from 2014 data and the ceasing of large (>60 km) north and south movements to define the completion of spring and fall migrations, respectively. For each pathway, we calculated 50%, 75%, 95%, and 99% BBMM confidence contours of each migration. After we calculated confidence contours in the

program R, we exported each into shapefiles and imported them into ArcGIS 10.2 (hereafter GIS; Environmental Systems Research Institute 2014). We created migration path maps by overlaying the 99% confidence contours from all PTT-tagged cranes for fall and spring migrations, resulting in 2 main corridors, 1 for each season, respectively. We created 1 “major” corridor that included data from all individuals and all migrations, except the notable outliers, which we later defined as minor corridors, to represent a cumulative LCRVP migratory corridor by overlaying all 99% confidence contours.

### Areas of migratory use

Once we mapped migratory pathways, we identified AMUs in ArcMap 10.2. Our data set lacked overall abundance of Sandhill Cranes at each area, as well as habitat information, and therefore did not fit specific definitions for “stopover” or “staging” (sensu Warnock 2010). Therefore, we created and used the umbrella phrase, “area of migratory use,” or AMU, to include all areas where the PTT-tagged cranes stopped during migration, which we defined as the individualized 75% confidence contour produced by BBMM. We isolated the 75% confidence contours and at least 2 subsequently time stamped locations within 40 km of each other to identify AMUs for fall (2014 and 2015) and spring (2014, 2015, and 2016) migrations. We only identified AMUs within the 75% confidence contours because we judged any locations outside this region to be population outliers. Because of numerous locations being close (within 40 km) to each other, we picked the central location within each cluster of locations ( $\geq 2$  locations) to represent each area and added a 40-km buffer to each central location to represent an AMU, which was then labeled by a flagship locality within the AMU, i.e., Mojave National Preserve. We ranked AMUs based on the number of cranes that used each, with 1 being the AMU with the greatest number of cranes and 21 being the AMU with the least number of cranes. If AMUs had the same number of cranes, then we considered the number of migrations (spring  $n = 3$ , fall  $n = 2$ ) that individuals used the area to break the tie. For AMUs that were still tied, we considered the number of total locations among all individuals within that AMU. If all previously described criteria did not rank individuals, they were considered tied. We ranked the AMUs to grade their relative importance.

### Migratory description statistics

We estimated distances cranes traveled during migrations by measuring the distance in ArcMap between an individual’s consecutive migratory locations used in the BBMM migration corridor analyses and compiling segment lengths. To assess migration duration, we calculated the number of days between the final location on a wintering or summer ground and the first location recorded at the corresponding terminus for each individual. Although we had multiple time stamps ( $\leq 4$ ) for each tagged crane on any given day, we rounded up to whole days because of the uncertainty of exact departure and arrival times caused by gaps between time stamps. We assessed the length of time (days and hours) spent at AMUs by subtracting an individual’s first PTT time stamp recorded within the boundaries of a given AMU from the last time stamp recorded in that same AMU in a migration. Gaps between time stamps cause uncertainty in exact time, so time spent at AMUs is the minimum duration there. Mean values were calculated for distance traveled,

duration of migration, and time spent at AMUs. Means were calculated for fall and spring migrations. Means for time spent at AMUs did not include time stamps for stays represented by only one location.

## RESULTS

### Capture

We attached PTTs to 16 adult cranes in January 2014, including 10 transmitters at Cibola NWR and 6 transmitters in the Imperial Valley. At the conclusion of summer 2014, we captured a single juvenile near Donnelly, Idaho, that survived through its first (fall) migration (Collins et al. 2016). An additional juvenile was trapped in July 2015 again near Donnelly, Idaho. Based on the migratory behavior and summering ecology of these juveniles, we included both in fall 2015 and spring 2016 LCRVP crane migratory corridor and AMU analyses. Location data for the entire project had about a 76% “success” rate, with about 24% of locations removed for analyses.

### Migration corridors

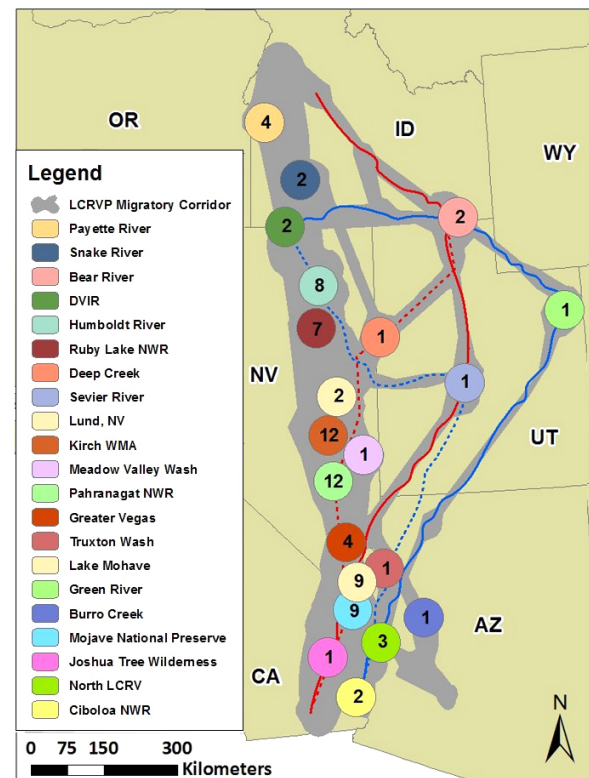
We used location data from 9 individuals in 2014 and 9 individuals in 2015 to delineate the fall migration corridor (99% confidence interval [CI]) and 14, 10, and 11 individuals from 2014 to 2016, respectively, to develop spring migration corridors (99% CI) for each year included in that interval. A generalized migration corridor was estimated based on combining fall and spring corridors (Fig. 2). Fall and spring migration corridors, with the exception of 2 tangents taken by 2 cranes, followed similar paths: a direct corridor between winter and breeding grounds that only varied among individuals by location of migration termini. The minor corridors, defined by simply being exhibited by a minority of the sample (1 individual used 2 minor corridors, another one used the third), were discovered through data from the Idaho juvenile trapped in summer 2015 and an adult crane captured at Cibola NWR, and both occurred during the fall 2015 migration. That adult crane had traveled another minor corridor during its spring 2015 migration, resulting in 3 minor corridors extending east into Utah. The major corridor for the remaining migrations was a direct north–south path between summering and wintering grounds, and the widest widths of each seasonal corridor were similar (fall = 151 km, spring = 146 km). From the farthest north boundaries to the farthest south boundaries, the fall and spring migration corridors were 1378 km and 1422 km, respectively. Farthest distances differed among seasons because LCRVP cranes did not always winter or summer or initiate migration in the exact locations as they did in prior migrations.

### Areas of migratory use

We identified 21 AMUs throughout the 5 migrations (Appendix 1; Fig. 2). The Wayne E. Kirch Wildlife Management Area (hereafter Kirch WMA) was ranked first with 12 individuals using it over the course of 5 migrations, with a total of 29.26 crane days. Twelve of 18 cranes stopped at Kirch WMA; however, each visit averaged only ~2 days. Pahrnagat NWR was ranked second with 12 individuals over the course of 5 migrations and for a total of 12.33 crane days (Appendix 1). Truxton Wash, Joshua Tree Wilderness, Burro Creek, and Deep Creek tied for the last rank, 17, with only 1 individual using each in 1 migration for less than 1 crane day each (Appendix 1). Seven AMUs were only used

during the spring migrations, and 5 different AMUs were only used in the fall migrations, all of which were used by  $\leq 2$  cranes (Appendix 1). Five AMUs were also summer termini for cranes, including Ruby Lake NWR, Lund, Humboldt River, Bear River, and Duck Valley Indian Reservation (DVIR), based on location data from summer. AMUs that exclusively held stays  $\leq 1$  day were Cibola NWR, Joshua Tree Wilderness Area, North LCRV, Mojave National Preserve, Lake Mohave, DVIR, Truxton Wash, Greater Vegas Area, Burro Creek, Deep Creek, and Sevier River. AMUs where some birds stayed longer than 1 day, but less than 1 week, included Pahrnagat NWR, Kirch WMA, and Snake River. Stays greater than 1 week were almost exclusively in known breeding areas during all migrations, including Humboldt River, Ruby Lake, Lund, NV, and Bear River AMUs. Payette River AMU in Idaho also had stays greater than 1 week, as did Green River along the typical Rocky Mountain population migration corridor and Meadow Valley Wash, but by fewer cranes.

**Fig. 2.** Map of migration corridors for the Lower Colorado River Valley population (LCRVP) of Greater Sandhill Cranes (*Antigone canadensis tabida*) plus 4 observed outlying paths taken by 2 tracked individuals. Crane “Cibola 006” is shown in blue, and crane “Idaho 005” in red. All 4 migratory trajectories were taken in 2015. Dashed lines represent spring migrations, and solid lines represent fall migrations. We include all areas of migratory use identified for the LCRVP. Numerals represent the number of different tracked individuals that visited the area at least once (for  $\geq 10$  hours). DVIR, Duck Valley Indian Reservation; LCRV, Lower Colorado River Valley; NWR, National Wildlife Refuge; WMA, Wildlife Management Area.



## Migratory descriptive statistics

Average distance traveled across all tagged cranes and migrations was 951 km (minimum = 648, maximum = 1544.36, standard deviation [SD] = 224.7, median = 915.35; Appendix 1). Average distance traveled during spring migration was shorter than fall migration distance average (spring = 935 km, standard error [SE] = 31.36, 95% CI [873.96, 996.89]; fall = 979 km, SE = 58.27, 95% CI [864.60, 1093.03]) but was not significantly shorter ( $P = 0.48$ ). The longest total distance traveled (path used, not necessarily a direct line) between winter and summer termini was 1544 km, and the shortest was 648 km (Appendix 1). Average durations for seasonal migrations coincided with average distances recorded with a shorter spring migration average of 13.7 days and a fall migration average of 22.5 days (also not significantly different,  $P = 0.12$ ). Time spent at AMUs varied within migrations and between events (fall vs. spring). The average stay at an AMU during the spring migrations was 3.3 days ( $n = 74$ , SD = 5.85, 95% CI [1.92, 4.63], median = 0.4). Average stay at an AMU during the fall migrations was 14.7 days ( $n = 25$ , SD = 19.46, 95% CI [6.70, 22.77], median = 1.4). Durations at AMUs were significantly different ( $P = 0.008$ ) between seasons.

## DISCUSSION

Variation in Sandhill Crane migration strategies across populations demonstrates the species' flexibility. Evolution arises from adaption; thus the predicted change in migration strategy, given resource availability, is likely to be expressed via changes in resource abundance across the various migration corridors. The characteristics of the LCRVP's migratory strategy best conform with the definition of a hop migration (Piersma 1987). MCP Sandhill Cranes exhibit a migration strategy between a skip and a jump, where MCP cranes leave winter grounds, stage on the Platte River in Nebraska, and either jump to the breeding grounds or hop to another staging area in Saskatchewan (Krapu et al. 2014). Fronczak et al. (2017) found that migration strategies of eastern population cranes vary but generally share definitive characteristics of a skip pattern. The individuals we tracked used 18 distinct AMUs along the ~1000-km major corridor and 3 additional AMUs along the minor corridors, with each crane making up to 6 and 4 recorded stops during spring and fall migrations, respectively. Typically, each crane spent a few days (3.3 days in spring and 14.7 days in fall; Appendix 1) at any one AMU, and migration duration varied widely among cranes (1–50 days in spring and 1–68 days in fall; Appendix 1).

Comprehensive research on migration resource availability or use has not been conducted on LCRVP cranes, despite concerns regarding the arid regions in their winter termini and along their migration corridor. AMUs consisted of both private agriculture (energy-rich row crops) and public WMAs (wetlands, some crops, and food plots) located within the boundaries of the Great Basin region. The Great Basin region contained several closed-system river and stream systems that typically had shallow, sandy, flat wetland habitats, often juxtaposed with agricultural regions (irrigation from nearby water bodies facilitates large agriculture operations in arid climates). The close proximity of necessary resources (food, drinking water, and roost sites) in the Great Basin region, and low population abundance, allowed the LCRVP to use it as its major corridor and also explains why Kirch WMA was the highest ranked AMU. LCRVP cranes roost and drink in

shallow wetland systems and forage in nearby alfalfa fields or wheat plots during migration along their major corridor in Nevada (most of the major migratory corridor is in Nevada). Alfalfa, a cash crop in Nevada, and insects found on the crop have high crude protein, which could supplement fat reserves obtained during the winter. Kirch WMA, located in the White River Valley, has multiple reservoirs, wet meadows, and food plots planted in winter wheat (Nevada Department of Wildlife 2018). These resource attributes, supplemented with the alfalfa planted in the White River Valley, make Kirch WMA very attractive for Sandhill Cranes. We speculate that high accessibility, abundance, energy content, and digestibility of food, for which alfalfa, grain, and tuber residual habitats have high potential, paired with the fewer numbers of LCRV birds could facilitate shorter stays at AMUs during migration, because less time is needed to acquire a large amount of energy resources.

LCRVP cranes limit time along their spring migration corridor to gain a competitive advantage on the breeding grounds. There is evidence for breeding range expansion for the LCRVP, and our data indicated that dispersal of several individuals into new areas could be a consequence of limited nesting habitat available on the traditional breeding grounds (Conring 2016). Baker et al. (1995) found that Sandhill Crane pairs only select habitat within 200 m of their nest. They defend their resources and do not allow other cranes to forage or roost within their breeding home range (Lewis et al. 1977). Adult Sandhill Cranes also exhibit high nest site fidelity (Drewien 1973, August 2011), returning to the same summer home range year after year. This suggests that, at least during spring migration, competition for nesting and brood-rearing territories on their breeding grounds may be the driver for the rapid migrations (13.7-day average spring migration [SD = 13.045]; Appendix 1) exhibited frequently. Krapu et al. (2014) suggested Arctic Circle snowmelt was one rationale for the long, rather slow (>3 months) spring migration of the MCP. Moreover, birds that breed at mid- to high latitudes time their arrival to summer grounds to avoid most, if not all, adverse weather and arrive when conditions are survivable (Carey 2009). The relatively lower latitudes for nesting in summer, compared with the MCP (Idaho and Nevada for LCRVP and Canada, Alaska, and Siberia for MCP), as well as lower elevation (within montane region) of nesting and brood-rearing habitats in summer, eliminate snowmelt as a major driver in AMU selection or other aspects of migratory ecology of the LCRVP in our study.

Resource availability along the migratory corridor is neither a limiting factor for the LCRVP nor the proximate reason cranes used multiple AMUs. The hop strategy, including the multiple stops at AMUs for short durations, may be driven by social behaviors. Stopping along a relatively short migration corridor provides opportunities for finding, establishing, or strengthening pair bonds. However, other populations require this same pair bonding, but not all exhibit the hop strategy. Sandhill Cranes are likely forging bonds opportunistically regardless of migratory strategy, either at many short-duration stops or at a few long-duration staging sites. The mechanisms underpinning the LCRVP migratory hop strategy are not yet certain, but our results suggest social drivers and subadult dispersal as possible causes.

Some marked cranes followed minor (not direct north–south) migratory corridors, and some did not show site fidelity to termini



every year (Conring 2016), supporting the possibility of dispersal via migrations. Dispersal and intermingling evidence for the Intermountain West populations is apparent (Collins et al. 2016). With the Rocky Mountain, LCRV, and Central Valley populations within close proximity to each other during summer, social mechanisms that result in dispersal of individuals, and subsequently genes, across the entirety of the Intermountain West are important for long-term conservation and highlight the importance of maintaining the AMUs for cranes in the western United States. LCRVP habitat use research on higher ranked AMUs could provide valuable information in regard to the specific resources that attract LCRVP cranes to those AMUs, which could serve as habitat management guidelines for the studied AMUs. By implementing researched habitat management efforts on all AMUs, not just the highly ranked ones, the apparent dispersal among the three Intermountain West populations of Sandhill Cranes would be better facilitated. The three western crane populations are currently regarded as distinct management entities, each having unique harvest guidelines and conservation statuses across states. As such, we highlight the importance of continuing comprehensive research on the extent of western Greater Sandhill Crane distributions to continue effectively assessing genetic diversity, impacts from harvest on discrete populations, and evaluation of conservation status across the distribution of the LCRV, Rocky Mountain, and Central Valley populations.

Responses to this article can be read online at:  
<http://www.ace-eco.org/issues/responses.php/1352>

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**Appendix 1.** Supplementary summary statistics tables.

Table A1.1. Areas of migratory use identified for the Lower Colorado River Valley Population of Sandhill Cranes (*Antigone canadensis tabida*) during all five migrations between spring 2014 and spring 2016. \*Areas of Migratory Use located along the minor corridors.

Ranking	Area of Migratory Use	Sum of Days	Migrations	Spring		Sum of Days	Migrations	Fall		Both Seasons	
				Cranes (18 max)	Years (3 max)			Cranes (18 max)	Years (2 max)	Sum of Days	Ave Duration (days)
1	Kirch WMA	20.47	13	10	3	8.79	2	2	1	29.26	1.95
2	Pahrnagat NWR	5.54	10	7	2	6.79	2	2	1	12.33	1.03
3	Mojave NP	3.1	8	7	3	0.42	2	2	2	3.51	0.35
4	Lake Mohave	2.79	7	6	3	0.58	2	2	1	3.38	0.38
5	Humboldt River	98.25	11	5	3	118.58	4	4	1	216.83	14.46
6	Ruby Lake NWR	33.08	7	5	3	6.79	1	1	1	39.87	4.98
7	Payette River	29.63	4	4	3	143.54	3	3	2	173.17	24.74
8	Greater Vegas Area	1.08	3	3	2	0.71	2	2	1	1.79	0.36
9	North LCRV	0.42	1	1	1	0	0	0	0	0.42	0.42
10	Cibola NWR	0	0	0	0	0.54	2	2	2	0.54	0.27
11	Lund NV	9.84	2	2	2	0	0	0	0	9.84	4.92
12	Snake River	2.05	2	2	2	0	0	0	0	2.05	1.02



13	Bear River*	0	0	0	0	58.5	2	2	1	58.5	29.25
14	DVIR	0.79	2	2	1	0	0	0	0	0.79	0.4
15	Green River*	0	0	0	0	25.42	1	1	1	25.42	25.42
	Meadow										
16	Valley Wash	7.42	1	1	2	0	0	0	0	7.42	7.42
16	Sevier River*	0	0	0	0	8	1	1	1	8	8
17	Joshua Tree	0	0	0	0	0.29	1	1	1	0.29	0.29
17	Truxton Wash	0.13	1	1	1	0	0	0	0	0.13	0.13
17	Burro Creek	0.42	1	1	1	0	0	0	0	0.42	0.42
17	Deep Creek	0.42	1	1	1	0	0	0	0	0.42	0.42

Table A1.2. Average Time Spent (Days) by Greater Sandhill Cranes (*Antigone canadensis tabida*) at Areas of Migratory Use (AMU) from Spring 2014–Spring 2016. \*NA indicates the site had no recorded visits

≥3 hours during that migration and were not included in averages.

Area of Migratory Use	Spring			Fall		
	$\bar{X}$	$\sigma_{\bar{x}}$	$n$	$\bar{X}$	$\sigma_{\bar{x}}$	$n$
Cibola NWR	NA	NA	NA	0.27	0.15	2
Joshua Tree	NA	NA	NA	0.29	0	1
North LCRV	0.42	0	1	NA	NA	NA
Mojave NP	0.39	0.02	8	0.21	0.08	2
Lake Mohave	0.4	0.05	7	0.29	0	2
Truxton Wash	0.13	0	1	NA	NA	NA
Greater Vegas Area	0.36	0.04	3	0.35	0.06	2
Pahrnagat NWR	0.55	0.15	10	3.4	2.98	2
Meadow Valley Wash	7.42	0	1	NA	NA	NA
Kirch WMA	1.57	0.41	13	2.96	2.83	2
Lund NV	4.92	4.5	2	NA	NA	NA
Sevier River	NA	NA	NA	0.33	0	1
Ruby Lake NWR	4.71	2.86	7	6.79	0	1
Green River	NA	NA	NA	25.42	0	1
Humboldt River	11.39	2.54	11	29.65	9.9	4
DVIR	0.4	0.02	2	NA	NA	NA
Bear River	NA	NA	NA	29.25	6.5	2
Snake River	1.02	0.6	2	NA	NA	NA
Payette River	7.41	4.26	4	47.85	8.1	3
Burro Creek	0.42	0	1	NA	NA	NA
Deep Creek	0.42	0	1	NA	NA	NA
All AMIs	3.27	0.68	74	14.74	3.89	25

Table A1.3. Migration routes used by satellite-tagged greater Sandhill Cranes (*Antigone canadensis tabida*) of the Lower Colorado River Valley Population.

Crane ID	Capture Date	Spring 2014	Fall 2014	Spring 2015	Fall 2015	Spring 2016
CIB001	1/1/2014	Major	Major	Unknown	Unknown	Major
CIB002	1/9/2014	Major	Major	Major	Major	Major
CIB003	1/9/2014	Major	Major	Major	Unknown	Major
CIB004	1/9/2014	Major	Unknown	Unknown	Unknown	Unknown
CIB005	1/9/2014	Major	Major	Major	Unknown	Major
CIB006	1/9/2014	Major	Major	<b>Minor</b>	<b>Minor</b>	Major
CIB007	1/14/2014	Major	Major	Unknown	Unknown	Unknown
CIB008	1/14/2014	Major	Major	Major	Major	Major
CIB009	1/14/2014	Major	Unknown	Unknown	Unknown	Unknown
CIB010	1/14/2014	Major	Unknown	Major	Unknown	Major
IV001	1/16/2014	Major	Major	Major	Major	Unknown
IV002	1/16/2014	Major	Major	Unknown	Unknown	Unknown
IV003	1/16/2014	Major	Major	Major	Major	Major
IV005	1/16/2014	Major	Major	Unknown	Major	Unknown
IV006	1/16/2014	Major	Major	Major	Major	Major
IV007	1/23/2014	Unknown	Major	Major	Major	Unknown
ID001	7/29/2014		Unknown	Unknown	Major	Major
ID005	7/30/2015				<b>Minor</b>	<b>Minor</b>

Table A1.4. Migration start and end dates, lengths (days), and distances (km) for our sample of satellite- tagged greater Sandhill Cranes (*Antigone canadensis tabida*) of the Lower Colorado Valley Population for fall migration.

Bird ID	Start	Arrival	Length (days)	Distance (km)	Fall
CIB001	8-Sep-14	14-Nov-14	67	1,310.06	2014
CIB002	27-Aug-14	14-Oct-14	48	858.51	2014
CIB003	31-Aug-14	3-Oct-14	33	988.64	2014
CIB004	29-Sep-14	3-Oct-14	4	990.43	2014
CIB005	1-Oct-14	2-Oct-14	1	780.5	2014
CIB006	30-Sep-14	3-Oct-14	3	987.81	2014
CIB008	31-Aug-14	14-Oct-14	44	804.83	2014
CIB010	30-Sep-14	2-Oct-14	2	774.04	2014
IV001	30-Sep-14	2-Oct-14	2	737.76	2014
IV003	29-Sep-14	2-Oct-14	3	681.22	2014
IV005	1-Oct-14	5-Oct-14	4	1,005.39	2014
IV006	30-Sep-14	3-Oct-14	3	917.33	2014
CIB002	11-Oct-15	23-Oct-15	12	786.85	2015
CIB006	16-Sep-15	8-Nov-15	53	1,544.36	2015
CIB008	8-Oct-15	10-Oct-15	2	851.97	2015
CIB010	3-Oct-15	7-Oct-15	4	842.87	2015
IV001	7-Sep-15	21-Sep-15	14	748.33	2015
IV003	2-Oct-15	3-Oct-15	1	721.67	2015
IV006	10-Sep-15	14-Oct-15	34	876.61	2015
IV007	17-Aug-15	24-Oct-15	68	1,433.50	2015
ID001	27-Sep-15	9-Nov-15	43	1,350.16	2015
ID005	3-Sep-15	23-Oct-15	50	1,541.01	2015
<b>Average</b>			22.5	978.81	
<b>Min</b>			1	681.22	
<b>Max</b>			68	1544.36	
<b>Median</b>	10/1/2014	10/29/2014	8	867.56	
<b>SD (sample)</b>			23.95	273.33	
<b>95% CI</b>					
<b>Upper</b>				864.06	
<b>95% CI</b>					
<b>Lower</b>				1093.03	



Table A1.5. Migration start and end dates, length of stay (days), and distances (km) for our sample of satellite-tagged greater Sandhill Cranes (*Antigone canadensis tabida*) of the Lower Colorado Valley Population for spring migration.

Bird ID	Start	Arrival	Length (days)	Distance (km)	Spring
CIB001	10-Mar-14	30-Mar-14	20	1,251.63	2014
CIB002	26-Feb-14	2-Mar-14	4	850.91	2014
CIB003	26-Feb-14	20-Mar-14	22	954.38	2014
CIB004	26-Feb-14	23-Mar-14	25	940.08	2014
CIB005	9-Mar-14	13-Mar-14	4	803.66	2014
CIB006	26-Feb-14	23-Mar-14	25	987.59	2014
CIB007	26-Feb-14	23-Mar-14	25	994.16	2014
CIB008	9-Mar-14	14-Mar-14	5	928.21	2014
CIB009	26-Feb-14	7-Mar-14	9	1,255.92	2014
CIB010	26-Feb-14	3-Mar-14	5	842.51	2014
IV001	23-Feb-14	26-Feb-14	3	664.84	2014
IV003	22-Feb-14	24-Feb-14	2	659.81	2014
IV005	23-Feb-14	26-Feb-14	3	1,009.45	2014
IV006	27-Feb-14	6-Mar-14	7	913.37	2014
CIB002	28-Feb-15	2-Mar-15	2	864.84	2015
CIB003	22-Feb-15	13-Mar-15	19	987.4	2015
CIB004	12-Feb-15	27-Mar-15	43	976.28	2015
CIB005	8-Mar-15	11-Mar-15	3	777.25	2015
CIB006	22-Feb-15	19-Mar-15	25	1,014.90	2015
CIB008	7-Mar-15	13-Mar-15	6	931.8	2015
CIB010	26-Feb-15	3-Mar-15	5	840.9	2015
IV001	25-Feb-15	6-Mar-15	9	716.63	2015
IV003	17-Feb-15	19-Feb-15	2	671.19	2015
IV006	26-Feb-15	11-Mar-15	13	847.6	2015
IV007	15-Feb-15	16-Mar-15	29	1,319.15	2015
CIB001	9-Feb-16	30-Mar-16	50	1340.66	2016
CIB002	29-Feb-16	3-Mar-16	3	879	2016
CIB003	2-Feb-16	12-Mar-16	39	945	2016
CIB004	25-Feb-16	30-Mar-16	34	971	2016
CIB005	8-Mar-15	11-Mar-15	3	794	2016
CIB006	25-Feb-16	20-Mar-16	24	1051	2016
CIB008	2-Mar-16	16-Mar-16	14	950	2016
CIB010	25-Feb-16	28-Feb-16	3	781	2016
ID001	1-Mar-16	20-Mar-16	19	1442.20	2016
ID005	29-Feb-16	5-Mar-16	5	1156	2016
IV001	23-Feb-16	29-Feb-16	6	731	2016
IV003	17-Feb-16	18-Feb-16	1	648	2016
IV006	1-Mar-16	5-Mar-16	4	853	2016
<b>Average</b>			13.68	935.43	
<b>Min</b>			1	648	
<b>Max</b>			50	1442.20	
<b>Median</b>	23-Feb-15	11-Mar-15	6.5	930.005	
<b>SD (sample)</b>			13.045	193.315	
<b>95% CI Upper</b>				873.96	
<b>95% CI Lower</b>				996.89	

